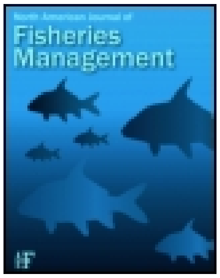

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Movement and Habitat Differentiation among Adult Shoal Bass, Largemouth Bass, and Spotted Bass in the Upper Flint River, Georgia

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Abstract
The Shoal Bass *Micropterus cataractae* is a fluvial specialist endemic to the Apalachicola River drainage in Alabama, Florida, and Georgia that has experienced declines throughout much of its range. The Flint River, Georgia, represents the largest remaining intact ecosystem for Shoal Bass in their native range. Spotted Bass *M. punctulatus* have recently been introduced into this system, causing concern about the potential negative impacts the species may have on the native populations of Shoal Bass and Largemouth Bass *M. salmoides*. To assess the symmetry and strength of competition and gain the greatest perspective on the interrelationships among these sympatric, congeneric species, we compared the movement patterns and habitat use of all three species of black bass present in this system. Fifteen Shoal Bass, 10 Largemouth Bass, and 6 Spotted Bass were implanted with radio transmitters in the Flint River and tracked for a period of 1 year (2008). Daily and hourly movements did not vary among species or season, though individuals of each species were observed moving >5 km to shoal complexes during spring. Habitat overlap varied between species during the study; overlap was highest between Spotted Bass and Largemouth Bass, intermediate between Spotted Bass and Shoal Bass, and lowest between Shoal Bass and Largemouth Bass. Shoal Bass tended to select coarse rocky habitat, while Largemouth Bass tended to select depositional habitat. Spotted Bass exhibited the widest niche breadth and generally used habitat in proportion to its availability. Use of similar habitats by these three species during the spring spawning period highlights the potential risk of genetic introgression of the two native species by introduced Spotted Bass. Physical barriers that restrict access to habitat during long-distance seasonal movements, as observed for several Shoal Bass in this study, may negatively impact populations of this species.

The introduction of nonnative fishes is recognized as a principal cause of the imperilment of native fishes throughout North America (Jelks et al. 2008). Interactions between nonnative and resident fishes are varied and include direct or indirect competition for resources such as shelter, food, or spawning areas, in addition to hybridization among closely related species (Whitmore 1983; Scoppettone 1993; Cucherousset and Olden 2011). The Shoal Bass *Micropterus cataractae* is endemic to the Apalachicola–Chattahoochee–Flint (ACF) River basin in Alabama, Florida, and Georgia (Williams and Burgess 1999). Populations of Shoal Bass are declining throughout much of their native range; as a result, the Shoal Bass is a species of high conservation concern in Alabama (Mirarchi et al. 2004), considered threatened in Florida (Gilbert 1992), and listed as

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vulnerable over its entire range by the American Fisheries Society (Williams et al. 1989; Jelks et al. 2008). Cited threats to Shoal Bass include habitat loss or degradation and the potential for competition and hybridization with introduced bass species (Williams and Burgess 1999; Wheeler and Allen 2003; Stormer and Maceina 2008). Significant declines in the distribution of Shoal Bass in Chattahoochee River tributaries (Stormer and Maceina 2008) prompted the Alabama Department of Conservation and Natural Resources to close the harvest of Shoal Bass in Alabama waters, the first such closure of a *Micropterus* fishery in the state (Maceina et al. 2007).

Shoal Bass are described as habitat specialists that associate with high-velocity, riffle-and-run habitats containing boulder and bedrock substrates in lotic systems (i.e., shoals; Wheeler and Allen 2003; Stormer and Maceina 2009). Although Shoal Bass are capable of surviving and even reproducing in ponds (Smitherman and Ramsey 1972), they do not persist in natural systems that have been impounded (Williams and Burgess 1999). Johnston and Kennon (2007) suggested that Shoal Bass require complex shoal habitats with a variety of microhabitats at various life stages in order to persist. Shoal Bass in unrestricted rivers appear to congregate in large shoal complexes to spawn (Sammons and Goclowski 2012), and high densities of age-0 Shoal Bass are typically found in these areas during the summer (Goclowski 2010), indicating that these habitats are also important nursery areas.

Spotted Bass *M. punctulatus* were first found in the ACF basin around 1941; these fish were found below the fall line defining the boundary between the Piedmont and Coastal Plain physiographic provinces (Williams and Burgess 1999). However, the species was slow to spread within the system, likely owing to the presence of numerous upstream dams, and specimens were not recorded above the fall line until 1968, possibly from a separate stocking event. As of 1999, Spotted Bass were distributed throughout the Chattahoochee River system but had not been found above the Albany Dam on the Flint River (Williams and Burgess 1999).

Although Shoal Bass did not occur naturally with Spotted Bass, they do occur sympatrically with the Largemouth Bass *M. salmoides* throughout their entire range (Williams and Burgess 1999). Wheeler and Allen (2003) found that adult Shoal Bass and Largemouth Bass in the Chipola River, Florida, had very similar diets; however, they used different habitats and appeared to coexist through habitat partitioning. The diets of Shoal Bass and Largemouth Bass in the Flint River, Georgia, showed little overlap, whereas the diets of Shoal Bass and Spotted Bass were more similar (Sammons 2012). Shoal Bass were more abundant in the shallower, faster-moving shoal areas in the Chipola River, Florida, while Largemouth Bass were more abundant in the deeper, slower-moving pools and backwater areas. The Spotted Bass has been described as a habitat generalist that often inhabits a variety of areas, including shallow rocky riffles and shoals (Hurst 1969; Vogele 1975; Tillma et al. 1998; Horton and Guy 2002). However, Shoal Bass and Spotted Bass had the highest relative abundances in shoal and riffle habitat in Alabama streams, where Spotted Bass have replaced Shoal Bass as the dominant bass species (Sammons and Maceina 2009). Although Spotted Bass in their native range have been shown to exist sympatrically with other black bass species through resource partitioning (Vogele 1975; Scott and Angermeier 1998; Sammons and Bettoli 1999), introductions of Spotted Bass into streams and reservoirs have been implicated in the decline of several native bass species, including Shoal Bass (Koppelman 1994; Pierce and Van Den Avyle 1997; Barwick et al. 2006; Stormer and Maceina 2008).

In recent years, populations of introduced Spotted Bass have become established in the upper Flint and Ocmulgee rivers in Georgia. Spotted Bass were first collected in the upper Flint River in 2005, and their numbers have increased rapidly throughout the river (J. Evans, Georgia Department of Natural Resources, personal communication). The recent introduction of Spotted Bass in the upper Flint River has caused great concern among anglers and fisheries managers about the potential negative impacts attributable to competition and hybridization of Spotted Bass with native black bass species. Thus, the objective of this study was to assess the potential for resource competition among the three bass species by examining the spatial and temporal patterns of movement and habitat use of adult fish co-occurring in a reach of the upper Flint River. At the time of the study, the relative abundances of all three bass species were similar, making it an ideal location at which to examine their resource use.

METHODS

Study site.—The Flint River flows 565 km from its headwaters near Atlanta, Georgia, to its confluence with the Chattahoochee River at Lake Seminole. This study was conducted along a 33.8-km stretch of the upper third of the Flint River, Georgia, from Flat Shoals (rkm 457.8) downstream to Sprewell Bluff State Park (rkm 424.0; Figure 1). This section of the river flows through the Piedmont physiographic province of Georgia and is characterized by a series of wide (up to 250 m), granite shoal areas with shallow water and higher current velocity interspersed with runs and pools exhibiting deeper water and lower velocity. The Flint River ranges from approximately 50–250 m in width throughout this section, with a mean annual discharge of 63.3 m^3/s at the U.S. Geological Survey (USGS) gauge located at Carsonville, Georgia (USGS site 02347500), approximately 40 rkm downstream of the study area. Major sport fishes occurring in the upper Flint River include Largemouth Bass, Shoal Bass, Spotted Bass, Channel Catfish *Ictalurus punctatus*, Flathead Catfish *Pylodictus olivarus*, and Redbreast Sunfish *Lepomis auritus*.

Telemetry and movement.—In December 2007, 11 Shoal Bass, 6 Spotted Bass, and 10 Largemouth Bass were collected using a boat-mounted DC electrofishing unit from the Flint River in the vicinity of the Georgia Highway 18 Bridge (Figure 1)

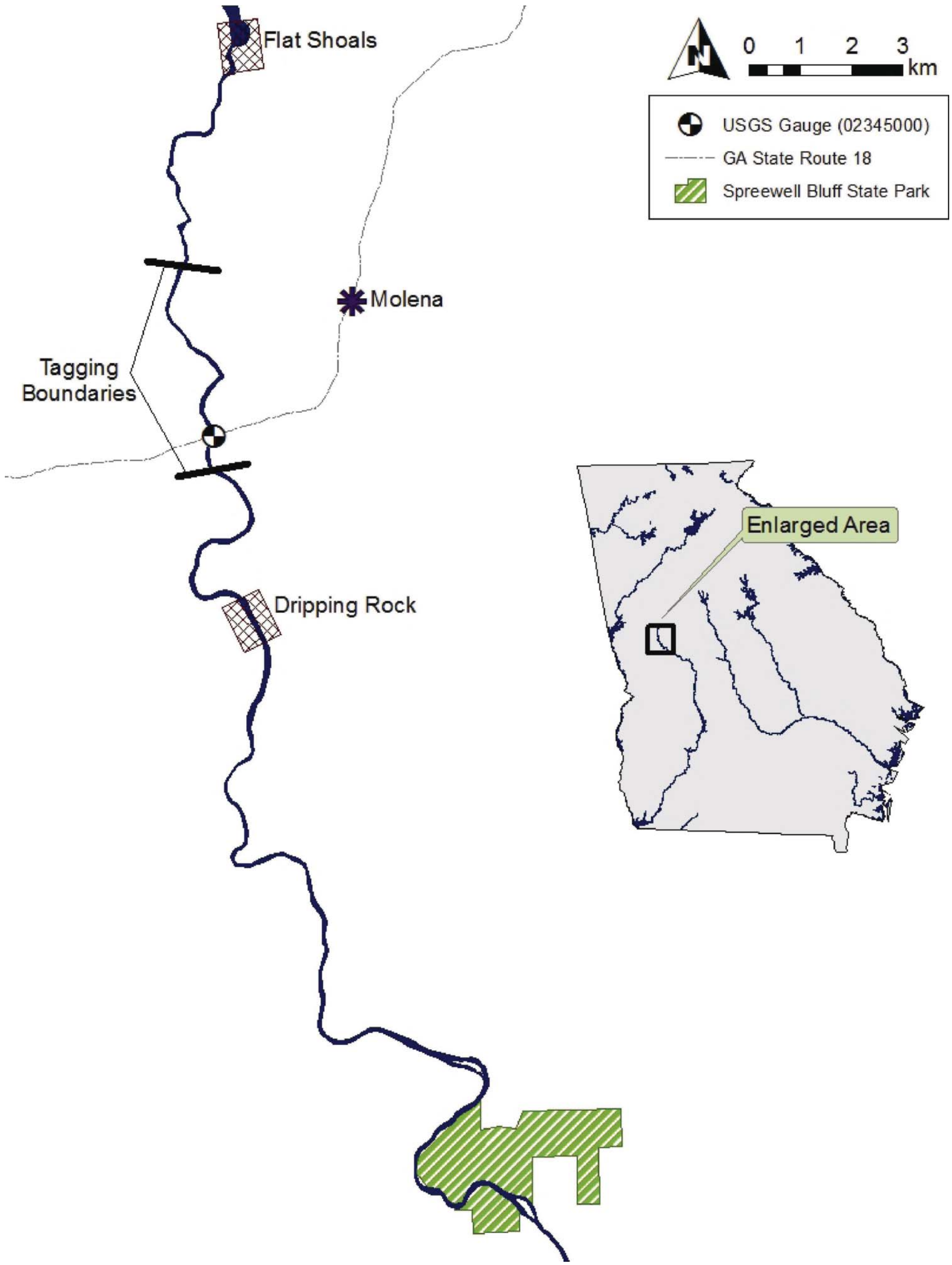

FIGURE 1. Map of the study site on the upper Flint River showing the area in which fish were tagged, along with the locations of major shoals, Sprewell Bluff State Park, and the USGS gauging station at the Georgia Highway 18 Bridge.

and surgically implanted with an Advanced Telemetry Systems (ATS) radio transmitter as described by Maceina et al. (1999). In June 2008, four additional Shoal Bass were captured in the same river section and implanted with transmitters recovered from fish that had died or shed their transmitters. Two size-groups of fish were used in this study. Fish weighing 180–700 g received 3.6-g radio transmitters (ATS Model F1580) with a 258-d battery life expectancy, whereas fish >700 g received 14-g transmitters (ATS Model F1835) with a 502-d battery life expectancy. Implanted transmitters were <2% of fish body weight in order to ensure that movement and behavior would not be affected (Winter 1996). The large transmitters were equipped with mortality sensors. The small transmitters did not have a mortality sensor, so mortality was assumed for any fish that did not move during three consecutive tracking events. Because Spotted Bass had become established in the Flint River only a few years prior to this study, no fish were collected that could be implanted with the larger-sized tags. Thus, only small Spotted Bass were used in this study.

Tracking activities commenced 2 weeks after surgery in January 2008 and were conducted approximately every 14 d until December 2008. To assess diel movements, fish were located every 6 h over a 24-h period during every other site visit (Sammons et al. 2003). Tagged fish were located by manually tracking the study reach by boat with an ATS Model R2000 receiver and directional yagi antenna. Fish locations were defined as the points at which the signal was strongest when the antenna was pointed directly at the water. The location of each fish was recorded using a Lowrance iFinder H20 Global Positioning System (GPS) unit, and time of day, water depth, velocity, and temperature were recorded at each location. During May 2008, an aerial reconnaissance of approximately 120 rkm was conducted using a fixed-wing aircraft fitted with two wing-mounted directional yagi antennae to locate fish that had left the study area. River stage and discharge data during tracking activities were obtained from the USGS gauge located at the Georgia Highway 18 Bridge near Molena (USGS site 02344872; Figure 1).

The daily movement rate of each fish was calculated in terms of minimum displacement per day by dividing the distance moved in meters between locations by the time elapsed (Colle et al. 1989; Wilkerson and Fisher 1997; Sammons et al. 2003). The diel movement rate of each fish located during the 24-h tracking sessions was similarly calculated in terms of minimum displacement per hour. Fish movement was compared among four seasons as defined by water temperature: winter, <12°C; spring, increasing from 12°C to 22°C; summer, greater than >22°C; and fall, decreasing from 22°C to 12°C (Todd and Rabeni 1989; Wilkerson and Fisher 1997; Sammons et al. 2003). Diel movement observations were pooled into two periods: day (the hours between sunrise and sunset) and night (the hours between sunset and sunrise). Mean daily and diel movement rates were $\log_{10}$-transformed to normalize the data and compared among seasons, species, and diel periods using a repeated-measures analysis of variance (ANOVA) with fixed (species, seasons, diel periods) and random effects (individual fish) (Maceina et al. 1994; Wilkerson and Fisher 1997; Bunnell et al. 1998; SAS 2002; Sammons and Maceina 2005). A Bonferroni correction ($P < 0.05/n$) was used for multiple comparisons among species, seasons, and diel periods.

TABLE 1. Classification scheme developed for the upper Flint River substrate map.

Substrate class	Definition
Sand	≥75% of area composed of particles <2 mm in diameter (sand, silt, clay, or fine organic detritus)
Rocky fine	>25% of area composed of rocks >2 mm but <500 mm in diameter across the longest axis
Rocky boulder	An area that includes >3 boulders, each >500 mm in diameter across the longest axis, each boulder within 1.5 m of the adjacent boulder. Any area meeting these criteria, regardless of underlying substrate, is classified as rocky boulder.
Bedrock	≥75% of area composed of bedrock or an outcropping with relatively smooth texture (not fractured into blocks >500 mm in diameter)
Mixed rocky	An area comprising two or more substrates classes (at least one being rocky) arranged such that no homogeneous portion is >10 m^2
No data	An area beyond the sonar range but within the boundaries of the river channel

Habitat mapping and analysis.—During March 2009, a single-pass sonar survey of the study area was conducted using a Humminbird 981c Side Imaging system at a frequency of 455 kHz and a range of 26 m (85 ft) per side, as described in Kaeser and Litts (2010). The survey began at the base of Flat Shoals (Figure 1) and continued 22 km downstream, encompassing all of the known locations of radio-tagged bass. These data were geoprocessed following the methods described in Kaeser and Litts (2010) to create a map of habitat features that included the predominant substrate types, river banks, and large woody debris. The substrates present in the surveyed reach were classified according to a scheme used during mapping of the lower 124 km of the Flint River (Kaeser et al., in press), with one modification; a general bedrock class replaced the two limestone bedrock classes present in the lower Flint River scheme (Table 1).

Habitat associations among the three species were investigated using a reduced data set that included only a single daytime observation (midday) per tagged individual per relocation survey in order to keep the time intervals consistent between observations. Observed fish locations were overlaid with the substrate, riverbank, and large woody debris layers in a GIS to extract habitat data from the map relevant to fish locations. The Euclidean distance from each fish location to the edge of the nearest polygon in each substrate class was calculated using the NEAR tool in ArcGIS 10 (ESRI 2007). A distance value of 0 was entered for the substrate class that contained the fish location. A similar approach was taken to calculate the distance of each fish location to the riverbank and the nearest piece of large woody debris. A distance-based approach was chosen for the habitat use analysis instead of a classification-based approach because some positional error (average, <10 m), attributable to the GPS equipment used during the study, was inherent in both the fish locations and map data (Kaeser and Litts 2010). A distance-based approach is not only robust to positional error (Conner et al. 2003) but also preserves the complexity of the information provided by a spatially complete (i.e., full-census) map of the habitat features throughout the study area. An index of substrate complexity within the vicinity of a fish location (hereafter referred to as the "edge") was generated by creating a 15-m buffer around each location and calculating the length of all substrate boundaries (i.e., lines) captured by each buffer. A count of the number of pieces of large woody debris present within each 15-m buffer was calculated in a similar manner. To conduct an inventory of the available habitat, a regular grid of points spaced 3 m apart was generated and habitat data were extracted from the map for each point as described above for all fish locations.

Depth and flow data were not incorporated into the multivariate habitat data matrix because several gaps in the data record occurred due to gear malfunction. Instead, differences between flow and depth were tested among species, seasons, and diel periods (fixed effects; the random effects consisted of individual fish) using mixed-model ANOVAs (SAS 2002). A Bonferroni correction was applied during all multiple comparisons of movement and habitat use.

Multiple-response permutation procedures (MRPP) were used to test for overall differences in multivariate habitat use among the three species. This procedure is a nonparametric approach that does not require the distributional assumptions of multivariate normality and homogeneity of variances (Mielke 1984; Zimmerman et al. 1985; Mielke and Berry 2001). Using MRPP, the null hypothesis of no difference between two or more groups is tested while simultaneously testing for differences in central tendency and dispersion. To avoid the issue of pseudoreplication inherent in treating telemetry locations as the sampling unit (Rogers and White 2007), median values were calculated for each habitat variable per individual, and these individual-based, median habitat vectors were examined during MRPP tests. Medians rather than means were selected for this analysis to reduce the influence of outlying observations of habitat use. To limit the analysis to individuals observed over the duration of the study, we included only those fish that had been located on >10 occasions in the MRPP data set. Sample sizes by species in the MRPP analysis were as follows: 8 Largemouth Bass, 6 Shoal Bass, and 6 Spotted Bass. The program BLOSSOM (Cade and Richards 2005) was used to execute the MRPP; test statistics were based on Euclidean distances to reduce the influence of outlying observations (Mielke and Berry 2001), and variables were commensurated using the mean Euclidean distance for each variable. Following a significant MRPP test, differences in multivariate dispersions were tested using a permutation version of a modified Van Valen's test in BLOSSOM (Van Valen 1978; Atkinson et al. 2010). Using MRPP, the global differences among all groups were tested first, followed by pairwise comparisons between species groups; tests were considered significant at a Bonferroni-corrected α level of 0.0125. The chance-corrected within-group (A) was calculated as described by McCune and Grace (2002), and reported as a measure of effect size. The Euclidean distance between commensurated, multivariate medians was calculated and used as a measure of the difference in central tendency between two species habitat use distributions; the average within-group distance to the multivariate median was used as a measure of dispersion (i.e., the breadth of habitat use).

Discriminant analysis was conducted to describe the pattern and degree of habitat partitioning along gradients defined by the habitat variables examined in this study and to compare ecological niches and niche overlap among species (SAS 2002). Given the descriptive purposes of this analysis, the observed locations of fish in the reduced data set were simply pooled by species. Discriminant analysis generates linear combinations of the environmental variables (i.e., discriminant factors) that maximize the variance among species while minimizing within-species variance, thereby identifying variables that best separate or uniquely define the niche of each species (McGarigal et al. 2000). As a single variable that represents a composite of multiple habitat variables, the first discriminant factor was used to calculate niche indices based on habitat association and availability. Hurlbert's B', an index that considers the variation in habitat availability, was used to describe niche breadth, and Hurlbert's niche overlap (L), a metric that describes the probability of interspecific overlap in habitat use relative to the frequency distribution of available habitat was used to describe potential niche overlap among the species (Hurlbert 1978). Chi-square analysis was used to determine whether species used habitats in proportion to their relative abundance by comparing the observed habitat use distribution of each species with the distribution of total available habitat as defined by the first discriminant factor.

RESULTS

Telemetry and Movement

A total of 27 tracking events were conducted over the duration of the study, resulting in a total of 677 fish locations. The reduced data set used to analyze multivariate fish habitat use included 120 Largemouth Bass locations, 67 Shoal Bass locations, and 83 Spotted Bass locations between January 4 and September 28, 2008. At the end of the study, 3 Largemouth Bass and 1

TABLE 2. Species (Largemouth Bass [LMB], Shoal Bass [SHB], and Spotted Bass [SPB]), total length, weight, number of days at large, number of locations, and fate of fish tracked in the upper Flint River during 2008.

Species	TL (mm)	Weight (g)	Days at large	No. locations	Fate
LMB	380	660	273	36	Tag expired
	337	461	146	13	Harvested by angler
	275	222	168	13	Consumed by bird
	324	367	253	35	Died
	247	180	168	22	Died
	394	850	370	46	Study ended
	478	1,389	370	45	Study ended
	426	937	369	45	Study ended
	392	770	167	16	Missing
	462	1,594	225	27	Died
SHB	258	212	273	17	Tag expired
	294	300	273	17	Harvested by angler
	345	471	168	18	Died
	279	252	25	1	Died
	342	520	273	30	Tag expired
	300	300	226	15	Harvested by angler
	508	2,040	156	4	Missing
	467	1,483	155	15	Died
	493	1,562	25	1	Died
	492	1,409	145	10	Died
	409	863	301	18	Missing
	392	875	126	13	Harvested by angler
	499	1,872	224	18	Died
	354	470	102	15	Tag expired
	415	851	169	19	Study ended
SPB	323	447	273	31	Tag expired
	261	210	224	26	Died
	281	202	302	41	Tag expired
	286	240	272	17	Tag expired
	260	207	271	36	Tag expired
	290	254	272	17	Tag expired

Shoal Bass with active transmitters remained in the study area. Of the remaining fish, 10 died or expelled transmitters, 9 were tracked until their transmitter battery failed, 4 were known to be harvested by anglers, 1 was consumed by a bird, and 3 were missing and never relocated during the study (Table 2).

All telemetered fish remained in close proximity to their original capture locations for most of the winter season. In late February and early March, individuals of all three species (3 of 10 Largemouth Bass, 10 of 11 Shoal Bass, and 3 of 6 Spotted Bass) emigrated from this region of the study area. Subsequent telemetry surveys and the aerial survey revealed that most of these fish had migrated 5–8 km toward large shoal complexes. Three Largemouth Bass moved upstream to the base of Flat Shoals, a large shoal complex located 9 km upstream from the Georgia Highway 18 Bridge (Figure 1); one Spotted Bass was located approximately 1 km below this shoal complex. Five Shoal Bass and two Spotted Bass moved downstream into Dripping Rock Shoals, a large shoal complex that began about 5 km downstream from the Georgia Highway 18 Bridge (Figure 1). Two additional Shoal Bass tags with mortality sensors engaged were found in close proximity to this shoal. During the aerial survey, one Shoal Bass was located in a shoal near Sprewell Bluff State Park, approximately 20 km downstream of its tagging location (Figure 1); this individual returned to the tagging area within 10 d of location by the aerial survey. Two emigrating Shoal Bass were unaccounted for until they returned to the study area in early May and June. All of the nonemigrating fish and all returning fish generally remained in close proximity to their tagging areas throughout the study.

The mean annual daily movement of tagged fish ranged from 178 to 430 m/d (Table 3) and was similar among species ($F = 2.77$; df $= 2, 25$; $P = 0.082$) or among seasons for each species ($F \leq 1.36$; df $\geq 3, 12$; $P \geq 0.21$; Figure 2). The mean annual diel movement of all species ranged from 76 to 119 m/h (Table 3)

TABLE 3. Annual mean movement rates, depth use, and flow use of radio-tagged black bass in the Flint River, Georgia during 2008.

	Largemouth Bass		Shoal Bass		Spotted Bass	
Variable	Mean (*n*)	SE	Mean (*n*)	SE	Mean (*n*)	SE
Diel movement (m/h)	119 (10)	43.6	97 (11)	30.8	76 (6)	17.6
Daily movement (m/d)	288 (10)	74	430 (11)	210	178 (6)	83.7
Depth (m)	1.69 (10)	0.06	1.64 (11)	0.10	1.86 (6)	0.01
Flow (m/s)	0.05 (10)	0.01	0.15 (11)	0.02	0.08 (6)	0.01

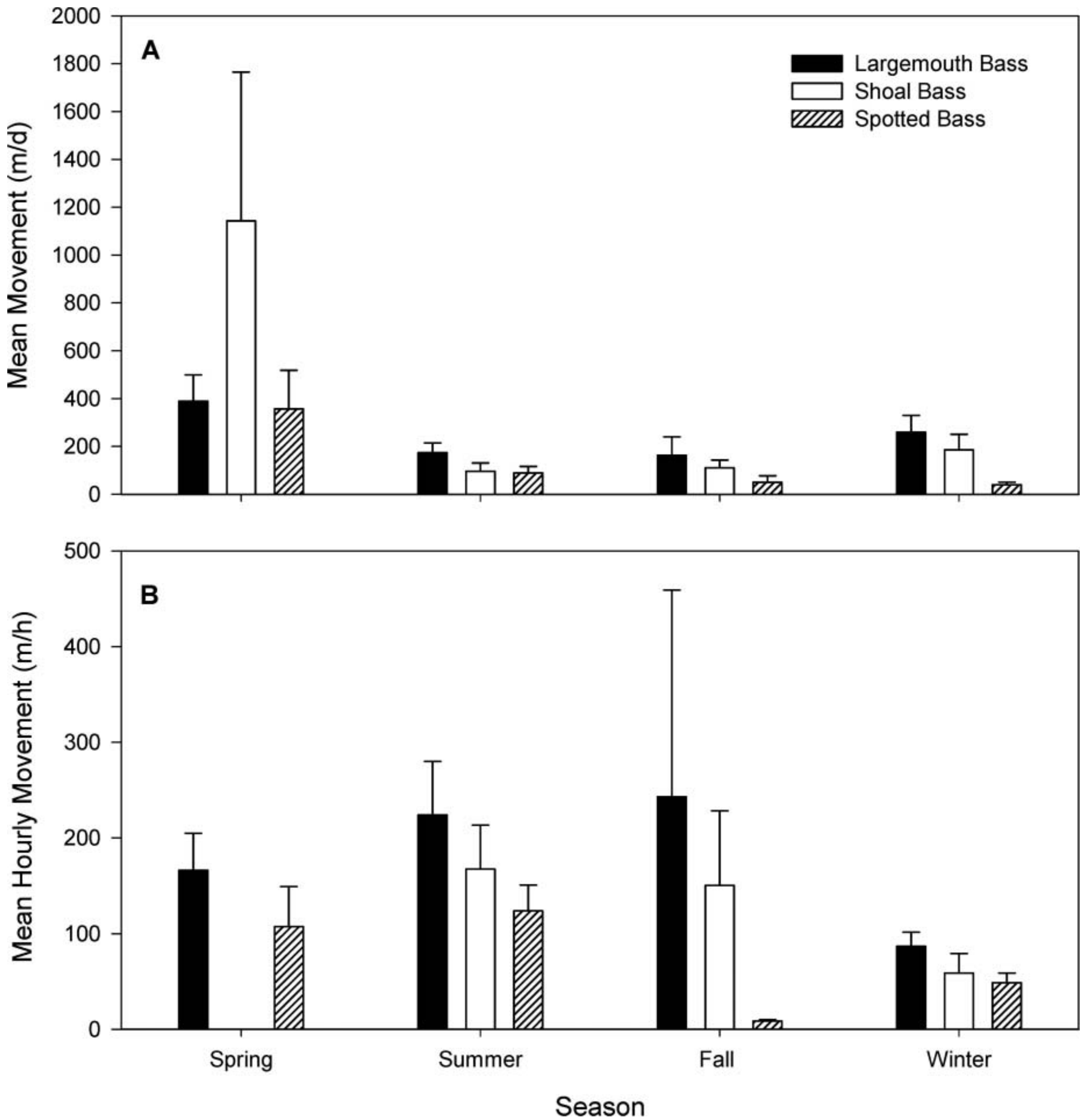

FIGURE 2. Seasonal mean (**A**) daily and (**B**) diel (hourly) movement rates of Largemouth Bass, Shoal Bass, and Spotted Bass in the upper Flint River in 2008. No Shoal Bass were observed in 24-h tracking events during the spring because they had all migrated out of the diel tracking area. The error bars represent SEs.

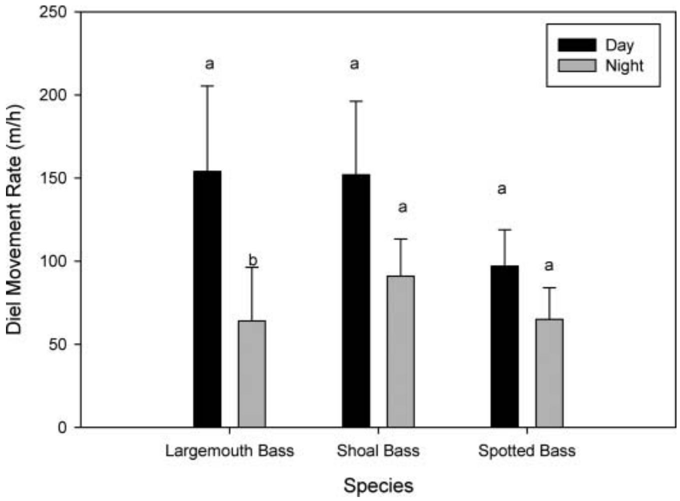

FIGURE 3. Movement rates of black bass in diel periods in the Flint River during 2008. Different lowercase letters denote significant differences between diel periods within species ($P \leq 0.05$); the error bars represent SEs.

and did not differ among species ($F = 0.31$; df = 2, 24; $P = 0.7329$) or among seasons for any species ($F \leq 4.58$; df $\geq$ 2, 3; $P \geq 0.06$; Figure 2). Diel mean movement was greater during daylight hours than at night for Largemouth Bass ($F = 6.44$; df = 1, 9; $P = 0.03$; Figure 3) but was similar between periods for Shoal Bass and Spotted Bass ($F \leq 3.20$; df $\geq$ 1, 6; $P \geq 0.10$; Figure 3).

Habitat Differentiation among Bass Species

The results of sonar habitat mapping indicated that the 99.7-ha study area had an overall substrate composition of 49% sand, 19% rocky boulder, 8% rocky fines, 14% bedrock, and 3% mixed rocky substrate. Missing data accounted for the remaining 7% of the area. A total of 3,117 pieces of large woody debris (LWD) were mapped throughout the study area. Most LWD was located near the stream margins, and LWD density was noticeably lower in coarse rocky areas than in runs and deeper reaches of the study area.

Habitat use differed among the three species (MRPP: $A = 0.079$; $P = 0.0065$; Van Valen's test: $P = 0.028$). The within-group dispersion for each species (Largemouth Bass = 1.52; Shoal Bass = 3.22; Spotted Bass = 2.08) showed that Shoal Bass had greater variation in habitat use among individuals than Spotted Bass and Largemouth Bass. Pairwise comparisons between species further suggested that the significant global MRPP test result was primarily attributable to differences in the central tendency of habitat use between Largemouth Bass and Shoal Bass (MRPP: $A = 0.131$; $P = 0.0011$; Van Valen's test: $P = 0.023$); the Euclidean difference in central tendency between the two species was 3.02. Pairwise comparisons between Largemouth Bass and Spotted Bass (MRPP: $A = 0.036$; $P = 0.116$), and Shoal Bass and Spotted Bass habitat use (MRPP: $A = 0.018$; $P = 0.236$) were not statistically significant. The difference in central tendency between the distributions for Largemouth Bass and Spotted Bass was 1.54, that between the distributions for Shoal Bass and Spotted Bass was 1.81.

The first discriminant factor had a relatively low eigenvalue (0.335) and low squared canonical correlation value ($R_c^2 = 0.25$), indicating the relatively low power of this function to discriminate among species based on the habitat variables examined. Likewise, the plot of species frequency distributions along the first discriminant axis illustrated that habitat overlap occurred among the fish observed in this study (Figure 4). Group means along the first discriminant axis were closely spaced (Largemouth Bass, –0.56; Spotted Bass, 0.11; Shoal Bass, 0.87), with the greatest separation occurring between the distributions of Largemouth Bass and Shoal Bass. The observed frequency of habitat use by Largemouth Bass and Shoal Bass differed from the frequency distribution of total available habitat in the study area (Largemouth Bass: $\chi^2 = 130$; df = 28; $P < 0.0001$; Shoal Bass: $\chi^2 = 64$; df = 28; $P = 0.0001$). The observed frequency of habitat use by Spotted Bass did not differ statistically from the distribution of total available habitat ($\chi^2 = 34$; df = 28; $P = 0.2200$).

The first discriminant axis represented an ecological gradient generally defined as depositional and woody on one end, and coarse rocky with less wood on the other (i.e., shoals with limited LWD; Table 4). A set of Largemouth Bass (40%) and Spotted Bass (20%) locations were associated with depositional areas comprised of sandy substrate and LWD at greater distances from rocky shoals (i.e., low scores on the discriminant axis); this multivariate habitat type was not used by Shoal Bass. Half of all observed locations of Largemouth Bass were within 3 m of sandy substrate (Table 4). Likewise, a set of Shoal Bass (22%) and Spotted Bass (7%) locations were associated with coarse rocky habitat, low abundance of LWD, and greater distance from depositional habitats (i.e., high scores on the discriminant axis); these locations occurred in the large downstream shoal used by Shoal and Spotted Bass during the spring spawning period (Figure 4; Table 4). Although the variable "distance to bedrock" did not contribute to the discrimination of species along the first axis, Shoal Bass clearly exhibited the strongest affinity for bedrock substrate (Table 4). Half of all observed Shoal Bass locations were within 15.6 m of bedrock substrate, compared with median distances of 56.8 m for Spotted Bass and 102.9 m for Largemouth Bass.

Hurlbert's niche breadth (B') was highest for Spotted Bass (0.749), next highest for Shoal Bass (0.611), and lowest for Largemouth Bass (0.435). Niche overlap between Largemouth and Shoal Bass was less than would be expected ($L = 0.785$) if both species used habitat in proportion to its availability; overlap was greater than expected ($L = 1.372$) between Largemouth and Spotted Bass. When Shoal Bass and Spotted Bass used the same habitats, their use was directly proportional to habitat availability ($L = 1.007$).

The distributions of the depths used were similar among species throughout the study (Kolmogorov–Smirnov test: KSa

TABLE 4. Within-species and total available habitat, multivariate median coordinates for habitat variables with respect to the reduced data set of 270 fish locations, and total canonical structure coefficients for habitat variables used to define the first discriminant factor (CAN1). All distance metrics, including the variable edge, are in meters. See Table 2 for species abbreviations.

Habitat variable	LMB	SHB	SPB	Total habitat	CAN1
Distance to sand	2.9	24.4	10.1	58.1	0.665
Distance to rocky fines	41.3	34.5	105.6	89.6	0.508
Distance to rocky boulders	189.2	149.4	140	192.8	–0.451
Distance to mixed rocky substrate	276.9	238.3	223.8	308.9	0.615
Distance to bedrock	102.9	15.6	56.8	92.2	–0.133
Distance to bank	9.8	16.4	11.9	14.6	0.131
Distance to LWD	10.1	18.2	10.5	23.2	0.473
LWD within 15-m buffer[a]	3.11	2.0	2.2	1.73	–0.562
Edge	36.6	43.3	37.1	34.6	–0.103

[a]Number of pieces.

< 1.31; $P \geq 0.0646$; Figure 5), and mean depth did not vary among Shoal Bass (1.64 m), Largemouth Bass (1.69 m), and Spotted Bass (1.86 m) ($F = 0.45$; df = 2, 26; $P = 0.6454$). The mean depths used did not vary among diel periods for any species ($F \leq 1.68$; df $\geq$ 3, 15; $P \geq 0.17$). Shoal Bass were more commonly found in flows >0.2 m/s and used a wider range of flow values than Largemouth Bass and Spotted Bass during this study (KSa > 1.62; $P < 0.0106$; Figure 5). Similarly, the mean flow used by Shoal Bass (0.15 m/s) was higher than that of Spotted Bass (0.08 m/s) and Largemouth Bass (0.05 m/s) ($F = 10.99$; df = 2, 26; Bonferroni-adjusted $P < 0.0413$), which were similar (Bonferroni-adjusted $P = 0.6067$). However, the

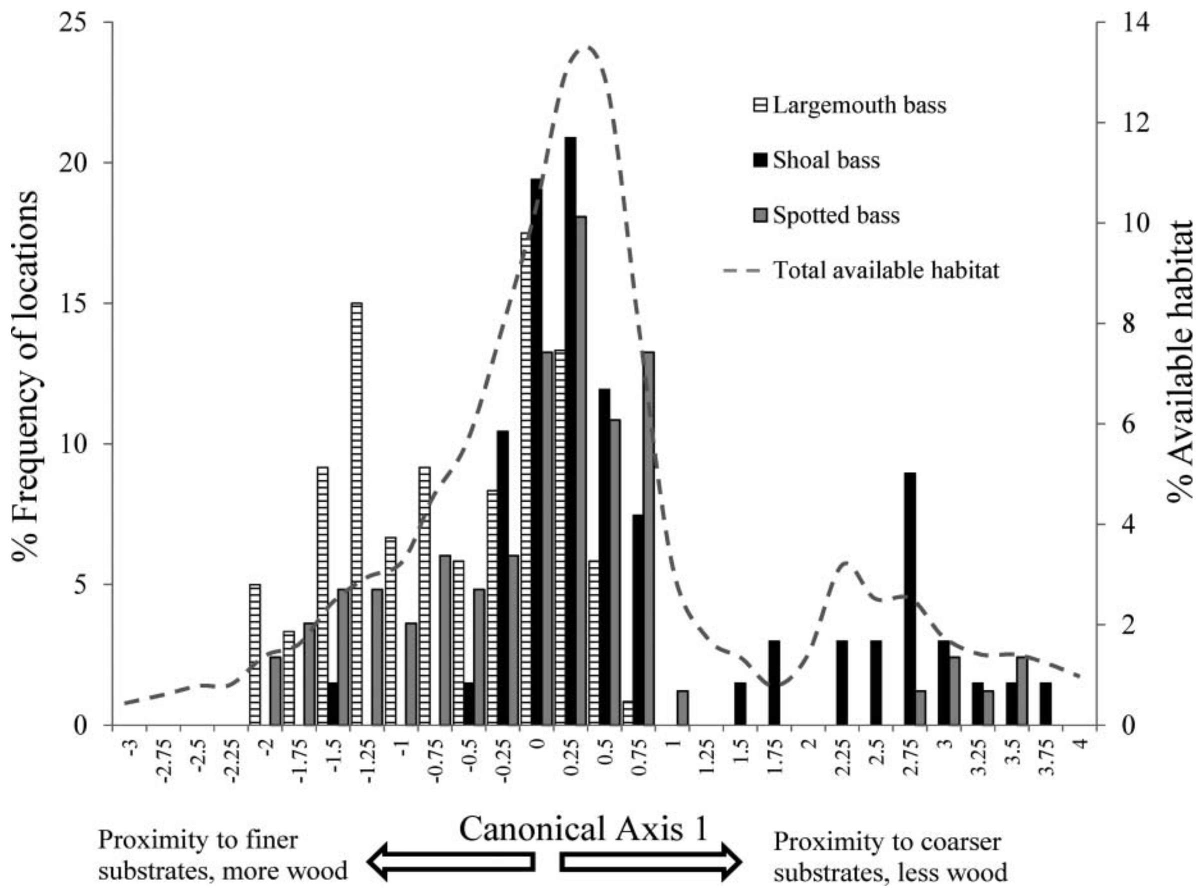

FIGURE 4. Frequency distributions of observed fish locations and total available habitat in the study area as defined by the first discriminant factor (canonical axis 1).

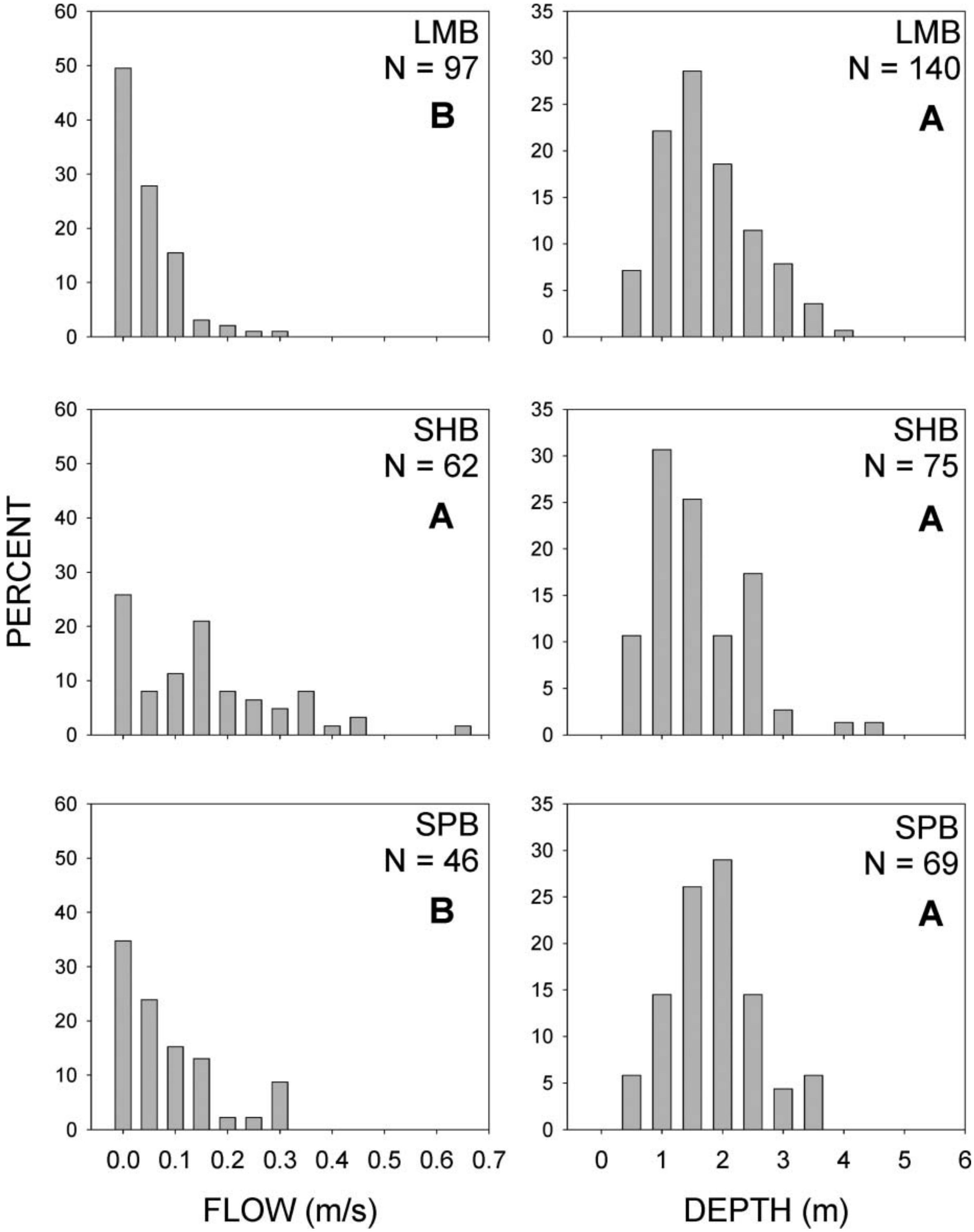

FIGURE 5. Distributions of depth and flow values used by radio-tracked Largemouth Bass (LMB), Shoal Bass (SHB), and Spotted Bass (SPB) in the upper Flint River during 2008. Distributions with the same letter were similar among species (Komogorov–Smirnov test; $P \leq 0.05$).

mean flow at fish locations did not vary among diel periods for any species ($F \leq 3.29$; df $\geq 3, 9$; $P \geq 0.0520$).

DISCUSSION

Movement

Mean daily movement rates did not vary among species or seasons during this study; however, the highest observed displacements occurred during the spring, when individuals of all three species moved distances in excess of 5 km, presumably to spawning areas. Seasonal differences in movement rates have been observed for several species of stream-dwelling black bass, including Shoal Bass (Stormer and Maceina 2009), Spotted Bass (Horton and Guy 2002), and Smallmouth Bass *Micropterus dolomieu* (Montgomery et al. 1980; Todd and Rabeni 1989; Langhurst and Schoenike 1990). Spawning migrations have been reported in some stream-dwelling basses, notably Smallmouth Bass (Montgomery et al. 1980; Todd and Rabeni 1989). In this study, all eight Shoal Bass and two of the Spotted Bass that were found outside of the study area during spring were located within, or in very close proximity to, major shoal complexes. Our observations suggest that large shoal complexes serve as important spawning and nursery areas for Shoal Bass and Spotted Bass in the upper Flint River. Similar spawning aggregations of Shoal Bass have been observed in shoal habitats during spring elsewhere in the Flint River (Sammons and Goclowski 2012; T. Ingram, Georgia Department of Natural Resources [GDNR], unpublished data) as well as in several tributary streams of the Chattahoochee River, Georgia (Sammons 2011; J. Slaughter, Georgia Power Company, unpublished data). The co-occurrence of Shoal and Spotted Bass in this habitat during the spawning season in the Flint River suggests that competition for nesting areas, genetic introgression, and interactions between these species at early life stages are potential conservation concerns.

The largest observed displacement in this study involved a Shoal Bass that was located approximately 20 km downstream from the study area during an aerial tracking survey. Within 10 d, this individual had returned to the study area, very close to its point of departure. This fish had not been located on tracking trips conducted through the same area as recently as 2 weeks earlier, indicating that it was further downstream. A related study of Shoal Bass on the Flint River documented spring upstream movements as great as 200 km (Sammons and Goclowski 2012). Similar upstream movements of 70–120 km have been found for Shoal Bass in the lower Flint River downstream of Albany, Georgia (T. Ingram, GDNR, unpublished data). Long-range movements (i.e., >50 km) have been documented for Smallmouth Bass in other river systems (Montgomery et al. 1980; Langhurst and Schoenike 1990), but spring spawning migrations of Shoal Bass may be unusually large for *Micropterus* spp. Although most of the Shoal Bass that emigrated from the study site remained near the shoals to which they moved, four of them returned to the study area during late spring or early summer. Each of these fish moved back to approximately the area where it had been located before emigrating; one of them actually moved back to the exact same rocky outcrop that it had inhabited before leaving and remained there for the duration of the study. Similar homing behavior has been observed for Smallmouth Bass in other studies (Todd and Rabeni 1989; Langhurst and Schoenike 1990; VanArnum et al. 2004).

As the Flint River experienced atypical low-flow conditions during 2008, the observed fish movements may have been less than normal. Low-water conditions during droughts can reduce habitat connectivity and restrict fish movements (Lake 2003; Schrank and Rahel 2006). Tagged Shoal Bass in the Flint River were commonly recaptured by anglers 60–100 km away from where they were tagged, and many of these large migrations were associated with high-discharge events (Sammons and Goclowski 2012). The return rate of these fish to their former home areas is unknown, but the low flows observed in summer 2008 may have restricted Shoal Bass movements and reduced the likelihood of additional fish exhibiting homing behavior during this study. A long-term telemetry study of a greater number of Shoal Bass may provide more insight into the seasonal movement patterns and homing behavior of Shoal Bass in the Flint River.

Habitat Use

Within our Flint River study area, distinct habitat differentiation was only evident between Largemouth and Shoal Bass. The habitat use of Largemouth and Shoal Bass differed from the distribution of available habitat, and niche overlap was lowest between the two species. Both Largemouth and Shoal Bass are native to the Flint River, so that partitioning may have evolved to support their coexistence (Wheeler and Allen 2003). Miller (1975) documented a similar occurrence of habitat partitioning among three sympatric black bass species in which Spotted Bass showed habitat preferences between those of Largemouth Bass and Smallmouth Bass: Largemouth Bass inhabited deep pools and quiet backwaters, Smallmouth Bass inhabited fast-moving waters, and Spotted Bass were found in intermediate areas in shallow pools near fast-moving water.

Spotted Bass are often described as habitat generalists (Hurst 1969; Vogele 1975; Tillma et al. 1998), and our results broadly support this characterization. Although Horton and Guy (2002) reported that Spotted Bass used pools more often than runs and riffles in Kansas streams and suggested that Spotted Bass prefer low-velocity environments, a very different pattern of habitat use by Spotted Bass was observed in the upper Flint River. Spotted Bass were found both in pools and in shoals, over depositional areas and within shallow rocky reaches of the upper Flint River. Spotted Bass (and Shoal Bass) exhibited high variation in habitat use, but only Spotted Bass used habitats in proportion to their availability. Spotted Bass habitat use broadly overlapped that of both Largemouth Bass and Shoal Bass, indicating that direct or indirect competition for resources may be imposed on both native species by the introduced Spotted Bass. Hurlbert's niche overlap was highest between Spotted Bass and Largemouth Bass because the adults of both species sometimes used a type of habitat that was not particularly abundant in the study area. This habitat type was represented by low scores on the first discriminant axis and could be described as sandy or rocky–fine reaches with high LWD abundance, far removed from shoal areas. Although Spotted Bass were associated with habitats used by both Largemouth Bass and Shoal Bass, these results suggest that the strength of competition is greater between Spotted and Largemouth Bass in the upper Flint River.

Large woody debris is an important component of many stream ecosystems. Instream wood provides stable substrate for aquatic invertebrate production (Angermeier and Karr 1984; Benke et al. 1985), offers fish refuge from strong current velocities (Crook and Robertson 1999), provides fish with cover in which to hide from predators and ambush prey (Angermeier and Karr 1984; Crook and Robertson 1999), and can play a large role in stream channel formation (Abbe and Montgomery 1996). Many studies have documented the importance of large woody debris to black bass in lotic environments (Todd and Rabeni 1989; Tillma et al. 1998; Horton and Guy 2002), although the relative importance of woody debris habitat does not appear to be consistent across species. Wheeler and Allen (2003) found that Largemouth Bass in the Chipola River, Florida, were associated with areas of higher than average woody debris index scores, whereas Shoal Bass presence was not related to woody debris index scores. Scott and Angermeier (1998) found that Spotted Bass in the New River, Virginia, occupied areas that featured woody cover, overhanging bank vegetation, and undercut banks, while Smallmouth Bass occupied rocky areas that lacked woody cover. We observed that all three species of black bass were located closer to, and near greater quantities of, LWD than would be expected from the total available habitat. Although the association between Shoal Bass and LWD was weaker than that for Largemouth and Spotted Bass, the association appeared to be context dependent. For example, when Shoal Bass were located within 5 m of rocky boulder habitat (a class of habitat that provides multidimensional cover), the median distance of fish to large woody debris was 62 m; when they were located near bedrock and all other habitats, the median distance of Shoal Bass to woody debris was 13 m, similar to that of Largemouth Bass and Spotted Bass. We infer from these results that Shoal Bass associate with LWD as cover when not closely associated with rocky boulder habitat. Shoal Bass farther downstream in the coastal plain of the Flint River are commonly found in close association with woody debris (J. Evans, GDNR, personal communication); thus, large woody debris can be important for the maintenance of Shoal Bass populations in these areas. The association of black bass with large woody debris emphasizes the importance of conserving this habitat feature and maintaining the processes responsible for recruiting woody debris to the stream system.

As expected, Shoal Bass were typically found using higher velocities than the other two species in the Flint River. However, the use of flows by Largemouth Bass and Spotted Bass were surprisingly similar throughout the study. Prevailing drought conditions resulted in abnormally low discharge levels (up to 87% below mean monthly discharge at USGS gauge 02347500) in the Flint River during the summer and fall of 2008. Low discharge levels may have reduced the heterogeneity of velocity levels throughout our study area, making it more difficult to detect differences in flow use among species during these seasons. Johnston and Kennon (2007) found that Shoal Bass in Little Uchee Creek, Alabama, used lower water velocities in summer during a dry year than they did during a wet year. If the Flint River study had been conducted during a wet year, more pronounced differences in flow use among species may have been observed, particularly during summer and fall.

Management Implications

Few Spotted Bass >350 mm were found in the Flint River during this study, and collecting fish >700 g for the larger tag sizes was not possible; thus, a low number of Spotted Bass in a small size range were used in this study. A different study design, one that either restricted all species to the available sizes of Spotted Bass or tagged larger Spotted Bass, may have resulted in different findings. However, we feel that this study provides managers with useful preliminary data with which to evaluate the effects of introduced Spotted Bass on congeneric species in a lotic system.

Drought conditions, as experienced in this study, physically reduce the habitat available for partitioning and intensify interactions between and within species (Matthews and Marsh-Matthews 2003). We observed that the habitat use of Spotted Bass overlapped with that of both Shoal Bass and Largemouth Bass and suspect that the intensity of overlap and concomitant competition for resources may have been elevated through an ecological crunch as described by Wiens (1977). Thus, under normal flow conditions, habitat overlap among these species, especially in terms of water velocity, may be much lower than was found during our study. However, agricultural, industrial, and residential uses of water in the Flint River watershed are high and increasing (Richter et al. 2003; Opsahl et al. 2007). The cumulative effects of water use can alter low-flow periodicity and longevity and either mimic or exacerbate natural drought conditions, leading to increased competition among aquatic organisms for reduced habitat and food and ultimately resulting in fish assemblage shifts and species declines (Richter et al. 2003; Freeman and Marcinek 2006; Johnston and Maceina 2009). The results from this study may indicate that the competitive effects among native and introduced black bass species are intensified during droughts. Although the long-term consequences of elevated competition could not be examined in this study, managers should be aware that continued increases in water use throughout this basin may favor Spotted Bass over Shoal Bass, particularly in smaller tributary streams (Stormer and Maceina 2008). Thus, Shoal Bass and Spotted Bass abundances throughout the Flint River basin should be monitored closely in the future.

Shoals are a critical habitat type for Shoal Bass in the Flint River, and they may serve as important spawning or nursery areas. Management efforts to protect the endemic Shoal Bass should focus on conserving shoal habitat and preserving connectivity throughout this unimpounded river reach. Shoal Bass form spawning aggregations in shoals during the spring, further emphasizing the need to protect these habitats and connectivity. Because both Shoal Bass and Spotted Bass were observed moving into shoal areas during the spawning season, there is the potential for introgressive hybridization between these species, which may alter the Shoal Bass gene pool and threaten the persistence of native stocks of the species. Native stocks of Guadalupe Bass *M. treculii* in Texas were threatened after the introduction of nonnative Smallmouth Bass into several streams. Researchers identified introgressive hybridization between the two species as the primary threat to the continued persistence of Guadalupe Bass (Whitmore 1983; Littrell et al. 2007). Similarly, native stocks of Redeye Bass *M. coosae* in South Carolina are threatened by introgressive hybridization with nonnative Alabama Bass *M. henshalli* (Barwick et al. 2006). Introduced Spotted Bass may pose a similar threat to Shoal Bass, as they have been found to hybridize with several black bass species in tributaries of the Chattahoochee River, including Shoal Bass and Largemouth Bass (Maceina et al. 2007). Further research should be conducted in the upper Flint River to assess the potential for long-term impacts related to hybridization.

The large-scale movements documented in this study, coupled with observations from an exploitation study and additional telemetry data on Shoal Bass from the coastal plain section of the Flint River (Sammons and Goclowski 2012), highlight the importance of connectivity throughout the Flint River for Shoal Bass. Shoal Bass in the river below Albany, Georgia, have been observed to move as much as 100 km to reach a spawning shoal complex located a few kilometers below a dam (T. Ingram, GDNR, personal communication). Above this dam is an extensive set of shoals that was likely the main spawning area for these fish before the dam was constructed. The GDNR has stocked Shoal Bass in this section of the river for the past two decades to bolster the low natural recruitment likely stemming from loss of connectivity and altered flow regimes. Currently, authorization of new dams on the upper Flint River is being discussed as a possible solution to the ongoing water allocation conflicts in the ACF River basin among Georgia, Alabama, and Florida (Jones 2008). Measures should be taken to prevent any new impoundments from being constructed on the Flint River, as the likely consequences would be less availability of prime spawning and nursery habitat, along with a concomitant reduction in gene flow. Evidence of the effects of impoundments on Shoal Bass has been seen in the Chattahoochee River system, where Spotted Bass thrive in the reservoir habitat and Shoal Bass persist in fragmented, relict populations below the dams (Sammons and Maceina 2009).

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